

OBSERVATIONS OF THE OCCURRENCE OF HYBRIDS BETWEEN TWO SYMPATRIC SPECIES OF FUCOID ALGAE

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ABSTRACT - Anderson's Hybrid Index method was used to identify plants of *F. spiralis*, *F. vesiculosus*, and hybrids between the two species collected from two areas of Great Cumbrae Island, Firth of Clyde, Scotland. Hybrids were found to be common in both of the sampled populations. A full range of hybrid forms were observed and these tended to be distributed such that *F. spiralis*-like types were found close to the *F. spiralis* zone, and *F. vesiculosus*-like types were found closest to the *F. vesiculosus* zone. It is suggested that failure to identify hybrids rather than their rarity is the most probable reason for the scarcity of references to them in the literature.

RÉSUMÉ - La méthode de l'indice d'hybridation d'Anderson a été appliquée pour identifier des thalles de *Fucus spiralis*, *F. vesiculosus* et leurs hybrides qui ont été échantillonnés dans deux sites des Îles de Great Cumbrae dans le Firth of Clyde en Ecosse. Il s'est avéré que les hybrides étaient communs parmi les deux populations échantillonnées. Tout un éventail de phénotypes hybrides a été observé avec une tendance à être distribués de telle façon que les formes proches de *F. spiralis* ont été trouvées au voisinage de la zone à *F. spiralis* et que les formes proches de *F. vesiculosus* ont été trouvées au voisinage de la zone à *F. vesiculosus*. Il semble que la difficulté de déterminer les caractères hybrides plutôt que leur rareté ait été à la base du manque de références sur ce sujet dans la littérature.

KEY WORDS - *Fucus vesiculosus*, *Fucus spiralis*, hybridisation, Scotland.

INTRODUCTION

It is a well established fact that individuals of the various species of *Fucus* exhibit a considerable degree of morphological variation both within and between populations (e.g. Russell, 1979, 1987; Norton *et al.*, 1981; Kalvas & Kautsky, 1993). For example the vesiculation of *F. vesiculosus* appears to bear some relation to vertical distribution on the shore, and both vesiculation and the dichotomising of plant fronds have been related to levels of exposure to rough water (Knight & Parke, 1950). However Kalvas & Kautsky (1993), studying populations of *F. vesiculosus* in the Baltic and North Seas, comment that, whilst morphological changes may be partly explained

by differences in wave exposure and salinity between their two study sites, it is not possible to rule out genetic differences (although they also conclude that it is unlikely that the variation observed within the population and between populations from the same area are genetically determined). Pollock (1969) concluded that there were genetic differences between the two forms of *Fucus distichus* which coexisted in the intertidal region of the San Juan Archipelago off the Pacific Coast of Washington, U.S.A. McLachlan *et al.* (1971) concluded that environmentally determined phenotypic plasticity is not the major factor for the very considerable morphological variation exhibited in nature, but rather, promiscuous hybridisation may be much more responsible. This proposition is supported by the fact that, upon closer examination of 'non-typical' specimens, they are often found to be non-typical because they possess the characteristics of two species. It is these plants which are reputedly hybrids.

Such plants have been reported in the wild and classified as hybrids between *F. spiralis* and *F. vesiculosus* (Sauvageau, 1909; Stomps, 1911; Kniep, 1925; Burrows & Lodge, 1951), between *F. vesiculosus* and *F. serratus* (Sauvageau, 1909), and between *F. vesiculosus* and *Ascophyllum nodosum* (Williams, 1899). *Fucus ceranoides* has also been reported as being involved in hybrid crosses with *F. spiralis* (Sauvageau, 1908; Gard, 1910). However, as Evans *et al.* (1982) comment, the validity of the term 'hybrid' is highly questionable without cytological or other evidence that the plants are the result of a cross between two distinct species. Unfortunately *Fucus* karyotypes appear to be indistinguishable (Evans, 1962, 1966) with a diploid chromosome number of $2n = 64$ and as Evans (1962) remarks, the uniformity in chromosome number, size and appearance in the various species may help to explain the ease with which hybrids are formed. Attempts to produce hybrids under laboratory conditions have been made on several occasions with varying degrees of success (Thuret, 1854; Williams, 1899; Kniep, 1925; Burrows & Lodge, 1953; Bolwell *et al.*, 1977). As a result of this work it seems certain that hybridisation on the shore is feasible and that hybrid plants should be expected in areas where two fucoid species grow in close proximity to one another.

Burrows & Lodge (1952) found hybrids between *F. spiralis* and *F. vesiculosus* in a study of fucoid populations growing in two disturbed areas - an area where the shore had been cleared of limpets (*Patella sp.*) and larger algal growth (at Port St. Mary, Isle of Man), and an area (in the Mersey estuary) where the rock surface flaked away, leaving bare areas open to recolonisation when attached plants reached a certain weight.

The aim of the present study has been to repeat that of Burrows & Lodge, but studying natural populations in relatively undisturbed habitats, to see whether hybrids occur in such situations and, if so, how frequent they are and how they are distributed in the population.

Algal nomenclature throughout this paper follows that of Parke & Dixon (1976).

METHODS

Populations of *Fucus spiralis* and *Fucus vesiculosus* were studied at two sites on Great Cumbrae Island, Firth of Clyde, Scotland in June 1993. Both sites had a very

shallow and uninterrupted gradient, the top of each transect being less than 1 m above its seaward end. Site 1 was at Balloch Bay on the east coast of the island. At this site there was a dense growth of fucoid algae on an area of bare rock at the top of the shore. Lower on the shore the substratum was composed of boulders embedded in a muddy seabed and algal growth was more spaced. Site 2 was at White Bay on the north coast of the island and comprised a rocky platform with a dense growth of fucoid algae at all levels. We were unable to estimate the depth of water at the two sites at high tide. However, given their proximity to one another (about 4 km) and the similarities in their gradient and flora we would assume their depths of seawater cover to be similar too.

Four transects, two 10 m apart at each site, were run down the shore from the top of the *F. spiralis* zone to the bottom of the *F. vesiculosus* zone and all plants attached to the substratum along the line of the transect were scored for seven different characters. Neither site could be described as being exposed and all plants of the *F. vesiculosus* type possessed some air bladders; there is no evidence to suggest the presence of populations of *F. vesiculosus* var. *vesiculosus*. The characters chosen were those used to distinguish the two species, as shown in Table I (the hybrid index method used being based on that of Anderson, 1949). Although receptacle dichotomy is recognised as a character by which *F. spiralis* and *F. vesiculosus* may be separated (Burrows & Lodge, 1951) we felt that this character was potentially the least reliable. However, in order to replicate as closely as possible the work of Burrows & Lodge (1951) we have included it. *Fucus spiralis* characters were scored as 0; *Fucus vesiculosus* characters were scored as 2. If a character seemed intermediate between these two extremes a score of 1 was entered. The scores for each plant were totalled. As a result, a minimum score of 0 was possible, and this represented a plant of *F. spiralis*, and a maximum score of 14 represented a plant of *F. vesiculosus*. These contrasting score values provide a standard of reference for assessing the intermediacy and variability of hybrid populations (Grant, 1981) and intermediate scores were taken to represent hybrids or back-crosses. In keeping with modern cladistical and phenetical procedures, no attempt was made to weight characters *a priori* (Sokal & Sneath, 1963; *contra* Burrows & Lodge, 1951).

| Character | <i>Fucus spiralis</i> | <i>Fucus vesiculosus</i> |
|--------------------|-----------------------|--------------------------|
| Thallus: | | |
| Shape | Spirally twisted | Flat |
| Air bladders | Absent | Present |
| Receptacles: | | |
| Shape ¹ | Rounded | Ellipsoidal pointed |
| Shape ² | No dichotomies | 1-2 dichotomies |
| Sterile rim | Present | Absent |
| Sex | Hermaphrodite | Dioecious |
| Sterile hairs | Protrude through | Do not protrude |
| | ostiole | through ostiole |

Table 1. Characters used to distinguish *Fucus spiralis* and *Fucus vesiculosus*.

RESULTS

Two 30 m transects were laid at each site, those at site 1 involved 35 and 33 plants (23 hermaphrodite, 30 male, 13 female and 2 unsexed immature) and those at site 2 involved 62 and 48 plants (52 hermaphrodite, 33 male, 24 female and 1 unsexed immature). G tests (Sokal & Rohlf, 1981) were used to compare the observed sex ratios with a 1:1 expectation. The results showed that males were significantly more common than were females in the site 1 population ($G = 6.83$, $p < 0.001$), but no such bias was apparent in the site 2 population.

Figure 1 shows the percentage of the plants at both sites which were found to have each of the possible hybrid scores. Kolmogorov-Smirnov tests (Sokal & Rohlf, 1981) were used to compare the distributions of hybrid scores within and between sites. Comparing transect 1 and transect 2 from site 1, the distributions of frequencies of scores do not differ ($D = 0.142$, $p < 0.001$), the same is true comparing transect 3 and transect 4 from site 2 ($D = 0.19$, $p < 0.001$). Given these results and the fact that the transects were only 10 m apart, and in an apparently homogeneous habitat the data collected were pooled to form one set per site. A Kolmogorov-Smirnov test to compare the distributions of the frequencies of scores from each site suggests that the two sites do not differ ($D = 0.203$, $p < 0.001$).

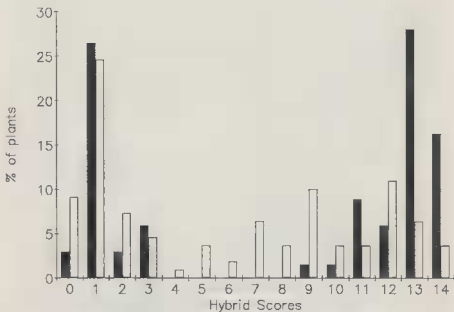


Figure 1. The percentages of plants of each hybrid score at site 1 (solid bars) and site 2 (open bars). For an explanation of hybrid score see text.

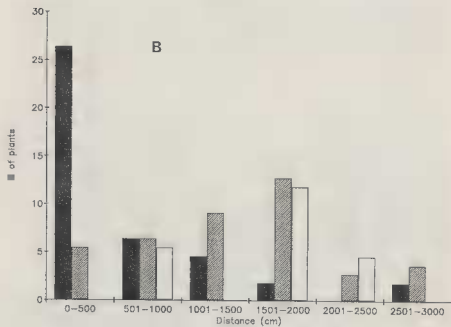
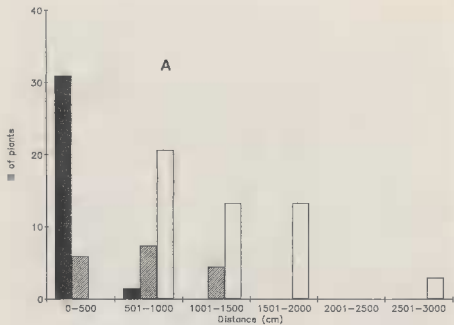
From Figure 1 it is apparent that, if rigorous criteria are used, 80.8% of plants at site 1 and 87.3% of plants at site 2 cannot be categorised as being typical *F. spiralis* or typical *F. vesiculosus*. If less rigorous criteria are used, and plants with scores of 0, 1 and 2 are considered to be *F. spiralis*, and those scoring 12, 13 and 14 to be *F. vesiculosus*, 17.7% of plants at site 1 and 38.2% of plants at site 2 cannot be categorised as being pure examples of either species. Thus intermediates, which can be assumed to be hybrids, are common at both sites. Plants scoring 1 or 2 (i.e. not strictly *F. spiralis*) have in almost all cases done so as a result of possessing receptacles which dichotomise to a greater or lesser extent; plants scoring 13 or 12 (i.e. not strictly *F. vesiculosus*) have either possessed a thallus with a tendency to spiralling or have had non-dichotomising receptacles.

Spearman's correlation coefficients (Sokal & Rohlf, 1981) were calculated to test the relationship between the position of plants on the shore (measured as the distance (cm) from the plant's holdfast to the top of the transect line) and their hybrid scores. The results of these analyses suggest that a strong relationship exists at site 1 ($r = 0.800$, $p < 0.001$) and that a less strong, but highly statistically significant relationship exists at site 2 ($r = 0.618$, $p < 0.001$). Thus there is a clear tendency for *F. spiralis*-type plants to be situated on the upper shore, and for *F. vesiculosus*-type plants to be situated on the lower shore. However, as figure 2 shows, this is not a clear cut relationship and considerable overlap exists. Figure 2 also indicates that plants having intermediate scores tend to occur around the area of overlap between the two presumed species type populations. At site 1 this area is small (between 0 cm and 1500 cm from the top of the transect line) presumably because the area of overlap between the species types is also small (between 500 cm and 1000 cm). At site 2 however, where the area of species type overlap is large (500 cm to 2500 cm), plants with intermediate hybrid scores are found along the entire transect (0 cm to 3000 cm).

DISCUSSION

It has been stated by Evans (1962) that the uniformity in chromosome number, size, and appearance in the various species of *Fucus* may help to explain the ease with which hybrids are formed. However, Burrows & Lodge (1951) comment on the very few instances on which naturally occurring hybrids have been recorded. For hybridisation to occur it is obvious that the fertile periods of the two species must overlap so that the gametes can mix: on this basis, hybridisation is much more likely between *F. spiralis* (fertile from October to June) and *F. vesiculosus* (fertile from March to May) than it is between the latter and *F. serratus* (fertile from October to December), although of course these fertile periods may be extended in various places due to the ambient environmental conditions.

Whilst it is not essential for populations of the two species to coexist, since gametes can be transported from their source of origin by water movements, there is a much higher probability of hybridisation resulting when the species are present together, and it is only in these circumstances that one might expect a hybrid population to develop. Kniep (1925) suggested that the most favourable position for hybrids would



be in the regions between the more sharply defined zones of the parent species, a view with which Burrows & Lodge (1951) disagree.

Although the two species overlap on the shore *F. spiralis* inhabits a zone on the upper shore and *F. vesiculosus* occupies the middle and lower shore. It might be expected, therefore, that hybrids which have a preponderance of *F. spiralis* characters will be found adjacent to the population of that parent, whilst those with a preponderance of *F. vesiculosus* characters will be found near that parent. This can be inferred from both the Spearman's correlation coefficients for the two sites and from the data presented in figure 2.

When examining plants in a hybrid swarm on the shore a complete range of intermediate morphologies exists between the two parent species: there could be a number of explanations for this. One possibility is that there is no linkage between the different characters selected for defining a species, and these may resultingly be inherited on an individual, random, basis. This would allow the existence of plants with any combination of characters. Alternatively, it is possible that what is being exhibited here is a situation where one is seeing the presence of fertile hybrids and of crosses between these hybrids and either other hybrids or the parent species so that the swarm is a mixture of parents, F1 and F2 (and so forth) generation plants. This question could only be answered by carrying out protein analyses of individual plants and was thus beyond the scope of the present study.

It could be suggested that the hermaphroditic condition of *F. spiralis* might enable this species to remain distinct (and not hybridise readily) more easily than a dioecious species such as *F. vesiculosus*. Due to the method of gamete liberation, *F. spiralis* eggs are in the presence of *F. spiralis* sperm from the moment of their release (since they are produced in the same conceptacles), whereas a dioecious species is dependent on attracting gametes from another plant. However, the results of this study give no indication that one species is more or less successful than the other. Studying hybridisation between *F. vesiculosus* and *F. serratus* Bolwell *et al.* (1977) found that, whilst cross fertilisation could not be detected with eggs released from freshly collected plants, levels of fertilisation up to 20% were detected with eggs freshly released from plants which had been stored for 5 to 7 days. This could suggest that hybrids arise in the wild where, for some reason, there is a shortage of sperm so that it takes longer than average for the eggs to achieve fertilisation. (Hence the finding of Bolwell *et al.* (1977) that a higher rate of cross-fertilisation was achieved with 'aged' eggs). This could indicate that male and female gametes mature at different times since there was no shortage of male plants in the populations studied (in the site 1 population, for example, there were twice as many male plants as female). It is known that female gametes liberate non-species specific sex attractants which would tend to promote cross-fertilisation were it not for the fact that the physico-chemical structure of the

Figure 2. The distributions (percentages of the population) of plants in each hybrid score class found in each distance class from the top of the transect line at site 1 (A), and site 2 (B). Solid bars represent plants scoring 0, 1 and 2; open bars represent plants scoring 12, 13 and 14; and hatched bars represent plants with scores between of 3 and 11.

surface of the egg appears to control species specific binding by sperms and should therefore promote intra-specific fertilisation (Green *et al.*, 1990). It is possible that as eggs 'age' over a period of time their surface physico-chemical structure may be altered, thus allowing the sperm of another species to effect fertilisation.

The reason for the relative absence of hybrids under natural conditions has been attributed to two possible causes. It may be that hybrids are generally absent from shores because they find the habitat unsuitable or are unable to compete with the germlings and/or established plants of the parent species (Kniep, 1925). Alternatively, hybrids may be present commonly on the shore but they have failed to be recognised because of the difficulty of studying such variable species (Sauvageau, 1909). The use of Anderson's Hybrid Index enables the easy recognition of plants intermediate between two parent species, and the present study indicates the abundant presence of hybrids. Moreover, neither of the sites studied in the present work are disturbed or open and so hybrids are obviously able to both survive in the habitat and to compete with established populations of the parent species. We would conclude therefore that, generally speaking, hybrids have not been recorded because they have failed to be identified, rather than because they do not exist.

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